# THE AMPHIPOD SUPERFAMILY LEUCOTHOIDEA ON THE PACIFIC COAST OF NORTH AMERICA: FAMILY AMPHILOCHIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

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**ABSTRACT**

Previous definitions of component genera and their probable relationships within the gammaridean amphipod family Amphilochidae were found to be unsatisfactory, necessitating realignment of taxonomic groupings within the northern hemisphere. ***Apolochus*** n. g., encompassing the Mediterranean regional type species *A. neopolitanus* (Della Valle, 1893), and *A. litoralis* (Stout, 1912), ***A. barnardi,*** n. sp., and ***A. staudei,*** n. sp. from the North Pacific region, is separated from *Amphilochus* Bate, 1862, based on the North Atlantic type species *A. manudens* Bate, 1862. ***Hourstonius***, n. g., based on the North Pacific type species *H. vilordes* (J. L. Barnard, 1962), is segregated from the Arctic and North Atlantic genus *Gitanopsis* Sars, 1895, based on *G. bispinosa* Boeck, 1871. Also redefined is *Gitana* Boeck, 1871, based on the Arctic type species *G. sarsi* Boeck, 1871, and including ***Gitana ellisi,*** n. sp., from the northeastern Pacific region.

Numerical analysis of 20 generic-level characters and character states suggests that *Hourstonius* and *Apolochus* are closely related, boreal and warm-temperate, North Pacific and North Atlantic generic complexes. By contrast, the primitive Arctic and North Atlantic genera *Gitana* Boeck, *Gitanopsis* Sars (sens. str.) and *Amphilochus* Bate (sens. str.) are closely related and possibly antecedent to the more advanced Mediterranean and "Pangean" genera *Amphilochoides* Sars, *Paramphilochoides* Lincoln, and *Amphilochella* Ledoyer. The diversity of eastern North Pacific species of Amphilochidae is below that of equivalent latitudes of the western North Pacific and eastern North Atlantic regions, but reasons for these differences are speculative.

## INTRODUCTION

Amphilochids are small, colourful, benthic leucothoidean amphipods commensal with sea fans, hydroids and other sessile marine invertebrates. During the past century and half of faunistic explorations of the Pacific coast of North America, only three species had previously been recorded, none prior to the turn of the century (Stimpson 1857; Stebbing 1906).

The first regional species was described from southern California by Vimy Stout in 1912. Three additional new species were described from California by J. L. Barnard (1962, 1969b). He also listed species from deeper waters and submarine canyons (1966), and described the ecological occurrence of species in the rocky intertidal of south-central California (1969b; 1975).

Among semi-popular accounts, Ricketts & Calvin (1968) included only "*Amphilochus neopolitanus*" among "common intertidal amphipod species" of the North American Pacific coast. Staude (1987) included four amphilochid species in lists and keys from the northwestern Pacific region, and Austin (1985) listed the same species from this general region, but none actually from the coast of British Columbia.

Gurjanova (1951) had listed amphilochids from the North Atlantic, Black Sea, and Arctic (Barents Sea) regions, and Shoemaker (1955) recorded *Gitanopsis arctica* from Pt. Barrow, Alaska. Barnard (1970) described several new taxa from the Hawaian archipelago. However, few amphilochid species had been recorded elsewhere in the North Pacific until the extensive work on Japanese coastal marine species by Hirayama (1983). These, and more recent records from Japan, were summarized in phyletic classification by Ishimaru (1994).

The present study encompasses the previously untreated amphilochid fauna of the Canadian Pacific and adjacent coastal marine regions and places it in the context of systematic concepts developed elsewhere.

## ACKNOWLEDGEMENTS

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## SYSTEMATICS

### AMPHILOCHIDAE Boeck

Amphilochidae Boeck, 1871: 107;—Stebbing 1906: 149;—Barnard 1962: 116;—Barnard 1969a: 132;—Lincoln 1979: 146;—Krapp-Schickel 1982: 70;—Bousfield 1982: 266.—Barnard & Karaman 1991: 92.

**Type Genus**: *Amphilochus* Bate, 1862 (N. Atlantic).

**Genera**:
North Pacific: *Gitana* Boeck, 1871; *Hourstonius*, n. g. (p. 11); *Apolochus* n. g. (p. 15); *Paramphilochus* Ishimaru & Ikehara, 1986; *Afrogitanopsis* Karaman, 1980 (Indian Ocean-Japan).
Extralimital: *Gitanopsis* Sars, 1895 (Arctic-N. Atlantic); *Amphilochoides* Sars, 1895 (N. Atlantic-Mediterranean); *Gitanogeiton* Stebbing, 1910 (Southwestern Pacific); *Amphilochopsis* Stephensen, 1925 (Arctic); *Amphilochella* Schellenberg, 1926 (Antarctic-Indian); *Rostrogitanopsis* Karaman, 1980 (S. African); *Cyclotelson* Potts, 1915 (Indo-Pacific). An undescribed genus is listed from the St. Lawrence estuary by Brunel et al. (1998).

**Diagnosis**: Body small, smooth; abdominal segments separate, generally unornamented. Anterior head lobe acute or rounded; rostrum distinct; eyes rounded. Antennae short; accessory flagellum minute or lacking. Flagellum of antenna 1 longer and more richly armed with aesthetascs in male.

Mouthparts modified: upper lip apically notched, lobes often asymmetrical; lower lip tall, inner margins often "notched", inner lobes essentially lacking. Mandible: molar various, often much reduced; spine-row strong; palp slender. Maxilla 1, inner plate small, outer plate strongly spined and/or toothed, palp 1- or 2-segmented. Maxilla 2 small, weakly setose. Maxilliped inner plate slender; outer plate broad; palp medium, dactyl not falciform.

Coxae 2-4 deep, increasing posteriorly; coxa 1 small, partly hidden by coxa 2. Gnathopods usually subchelate, often dissimilar in form and size, not sexually dimorphic. Gnathopod 2 usually the larger; posterior

**KEY TO NORTH PACIFIC GENERA OF AMPHILOCHIDAE (see also Fig. 1)**

1. Peraeopods 3-7 prehensile; gnathopod 2 sexually dimorphic ..... *Afrogitanopsis* (Japan)
   Peraeopods 3-7 ordinary, ambulatory; gnathopod 2 similar in both sexes ..... 2.

2. Telson elongate, sharply acute, apex minutely dentate; coxae 2-4, lower margin serrate; accessory flagellum lacking or very minute..... 3.
   Telson apex smoothly and sharply rounded, rarely acute; coxae 2-4, lower margin smooth; accessory flagellum small, 1-segmented ..... 4.

3. Gnathopod 2 distinctly parachelate, propod large; maxilla 1, palp 2-segmented; mandibular molar not triturative ..... ***Paramphilochus*** (Japan)
   Gnathopods 1 & 2, propods small, nearly simple, palm weakly (or not) distinct from hind margin; maxilla 1, palp 1-segmented; mandibular molar normally large, triturative (Fig. 1B) .... ***Gitana*** (p. 6)

4. Mandibular molar large, triturative, with marginal fringe of slender spines (Fig. 1c); gnathopod 1, propod broadening distally, sub-triangular; peraeopod 5, brood lamella longer than basis, with 8+ marginal setae; peraeopods 3 & 4, dactyls medium, slender ..... ***Hourstonius*** (p. 11)
   Mandibular molar vestigial, triturating surface weak or lacking; gnathopod 1, propod slightly (or not) broadening distally, anterior margin convex; peraeopod 5, brood lamella small, with 5-6 marginal setae; peraeopods 3 & 4, dactyls short ..... ***Apolochus*** (p. 15)

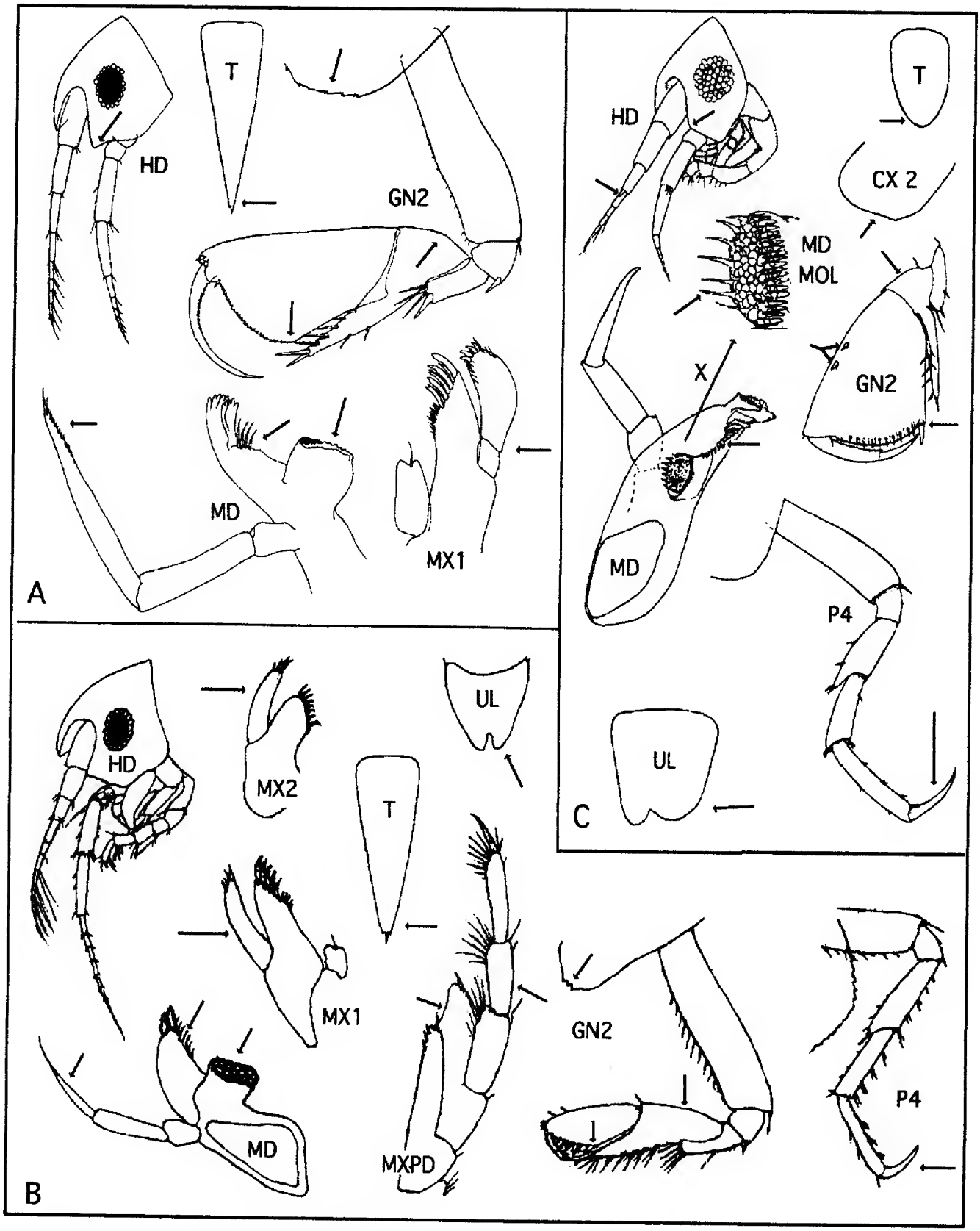


Fig. 1. Characters and Characters states of *Gitanopsis*, *Gitana*, and *Hourstonius*. A. *Gitanopsis inermis* (modified from Lincoln (1979). B. *Gitana sarsi* (modified from Sars (1895); C. *Hourstonius laguna* (after McKinney 1978). **[see p. 28 for figures legend]**

lobe of carpus typically extended forward behind propod. Coxae 5-7 deep, regularly postero-lobate. Peraeopods slender. Peraeopods 5-7 usually subsimilar in size and form; segment 4, posterodistal process not strongly overhanging segment 5.

Uropods slender, rami narrowly lanceolate. Uropod 2 small, rami unequal, rarely exceeding elongate peduncle of biramous uropod 3. Telson longer than wide, distally (sub)acute, minutely tridentate, or rounded, weakly (or not) keeled below,

Brood plates broad, decreasing posteriorly, margins long-setose. Coxal gills simple, on pereopods 2-6.

**Remarks**: Family Amphilochidae is a member of superfamily Leucothoidea, closely related to family Pleustidae (see Bousfield 1983; Bousfield & Shih 1994). Character states of coxal plates and uropods are also superficially similar to those of family Stenothoidae near which it often closely positioned (e.g., Stebbing 1906; Barnard 1962). Barnard & Karaman (1991) include family Amphilochidae within an amphilocoid group that encompasses families Cyproideidae, Pseudamphilochidae, and Bolttsiidae.

Family Amphilochidae presently encompasses 13 genera and about 70 species world-wide. A further yet undescribed genus, based on an undescribed *Gitanopsis*-like species, is listed tentatively from the St. Lawrence estuary by Brunel et al. (1998, p. 187). All but 5 essentially monotypic genera and about 85% of the species are endemic to the northern hemisphere. On this basis, and cognizant of the need for more realistic recognition of natural relationships, the partial realignment of North Pacific and North Atlantic species of *Amphilochus* Bate, sens. lat. and *Gitanopsis* Sars, sens. lat. would appear justified at this time [see Discussion and figs. 8-10].

### *Gitana* Boeck

*Gitana* Boeck, 1871: 132;—Stebbing 1906: 155;—Chevreux & Fage 1925: 118;—Gurjanova 1951: 302;—Lincoln 1979: 162;—Krapp-Schickel 1982: 82, key;—Barnard & Karaman 1991: 96.

**Type species.** *Gitana sarsi* Boeck, 1871, designated by Sars 1895: 229.

**Pacific Species:** *Gitana abyssicola* Sars, 1895 (N. Atlantic); *G. calitemplado* Barnard, 1962 (California); *G. liliuokalaniae* Barnard, 1970 (Hawaii); *G. bilobata* Myers, 1985 (Fiji); *G. gracilis* Myers, 1985 (Fiji); *G. ellisi*, n. sp., (British Columbia).

**Extralimital species**: *G. sarsi* Boeck, 1871 (N. Atlantic); *G. rostrata* Boeck, 1871 (N. Atlantic); *G. longicarpa* Ledoyer, 1977 (Mediterranean); *G. dominica* Thomas & Barnard, 1990 (Caribbean).

**Diagnosis:** Anterior head lobe acute or rounded. Antennae unequal in length; accessory flagellum lacking or very minute.

Upper lip, lobes symmetrical. Lower lip, inner shoulders with sharp notch. Mandibular molar large, cushion-shaped, triturative; spine row moderate, 5-9 blades; palp segment 3 not elongate. Maxilla 1, palp 1-segmented. Maxilla 2, inner plate stout. Maxilliped, inner plate with two stout medially curved spines; inner margin of outer plate weakly excavate; palp segment 1 equal to segment 2.

Coxae 2 weakly serrate posterodistally. Gnathopods 1-2 small, weakly subchelate or simple; palm very oblique, dactyl often pectinate posteriorly. Peraeopods slender; dactyls relatively long.

Pleome side plate 2, hind corner squared or obtuse. Uropod 3, ram short, margins bare or nearly so. Telson long, tapering, apex acute, usually minutely tridentate.

Coxal gills small. Brood plates variable, usually large on peraeopods 2 and 3.

**Distribution:** Pan arctic-boreal , N. Atlantic and N. Pacific, extending southwards into warm-temperate and tropical regions, in depths of 0-578 m.

**Remarks**: *Gitana* as presently defined, exhibits considerable morphological variation, especially in gnathopods, mouthparts and brood plates. Tropical species (e.g., *G. dominica*) show mouthpart character states similar to *Hourstonius* but a full revisionary analysis is outside the scope of the present study.

### *Gitana ellisi* new species
(Fig. 2)

**Material examined.**

**British Columbia,** Southern Vancouver Island:
ELB Stn. B21b, off Brady's Beach, Vancouver I. (48°,50'N, 125°,09'W), on sand, algae, 10-20 m, dredge, June 1, 1977. - ♀ ov. **holotype**, slide mount; 2 ♀♀ **paratypes**; slide mount, NMCC1992-0242. Ibid. - 2 ♀♀ **paratypes**, NMCC1992-0243.
Victoria region, Saanich Peninsula (48°N, 123°W) (KEC Stn.?, no other data), 1981 - 2 ♀♀, NMCC1992-0252.

**Diagnosis:** Female ov (3.0 mm) holotype: Rostrum medium, apex slightly down curved. Eye large, black,

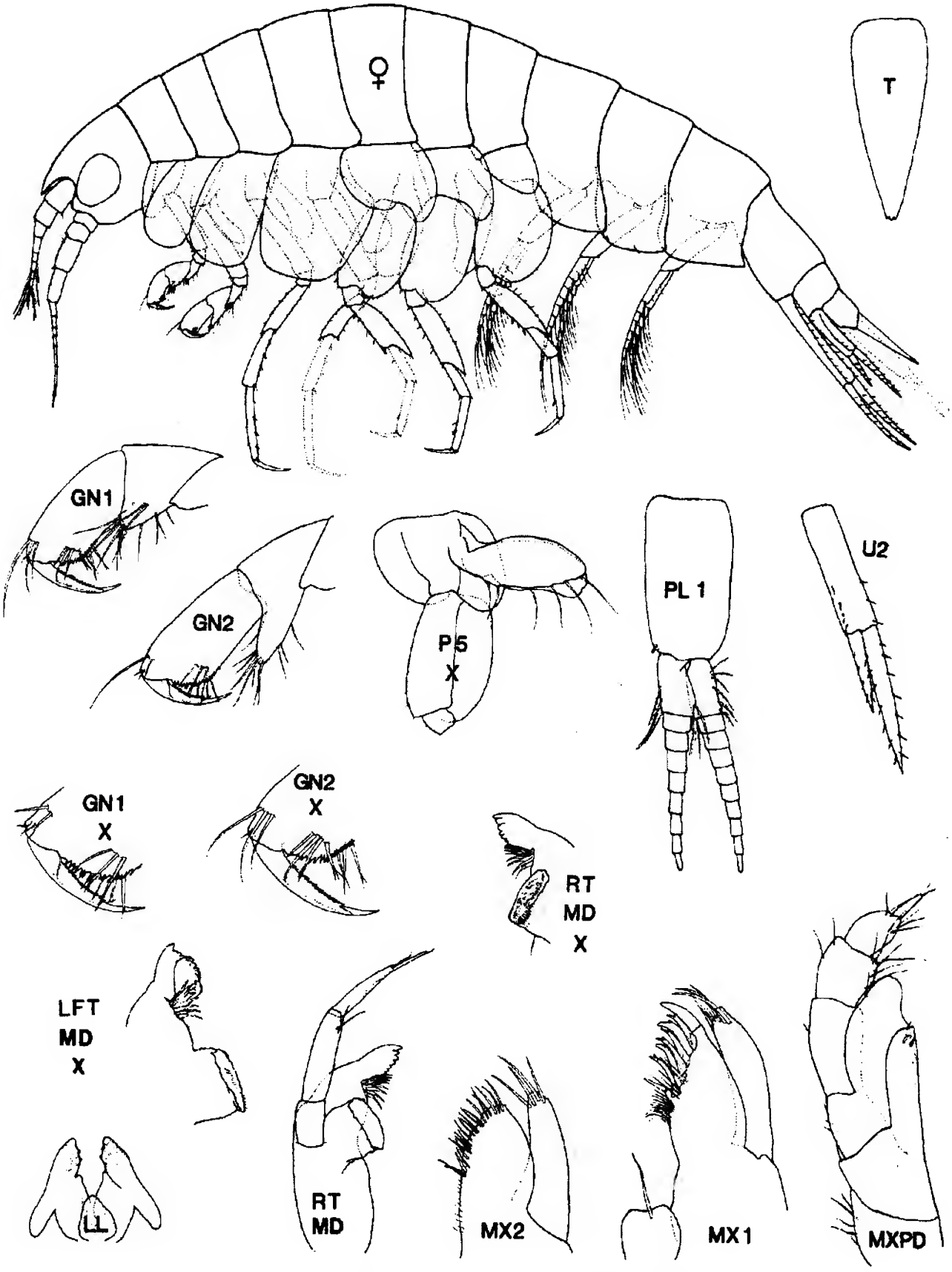


Fig. 2. ***Gitana ellisi***, n. sp.. ♀ ov. ( 3.0 mm). Off Brady's Beach, Vancouver I., B. C.

**Key to North Pacific and some North Atlantic species of *Gitana*.**

1. Head lobe acute; coxa 2, lower margin sharply rounded, serrate medially; brood plates large . . . 2.
   Head lobe rounded; coxa 2 smooth below or serrration postero-distally; brood plates small . . . . . 3.

2. Gnathopod 2, carpal lobe < 1/4 propod); peraeopod 7, basis widest medially . . . . *G. abyssicola* Sars
   Gnathopod 2, carpal lobe, length >1/2 propod; peraeopod 7 basis widest distally . . *G. sarsi* Boeck

3. Gnathopods 1 & 2, propodal palm short, distinct, oblique . . . . . *G. ellisi* n. sp. (p. 6)
   Gnathopods 1 & 2, palm elongate, horizontal, continuous with posterior margin . . . . . 4.

4. Gnathopds 1 & 2, propod distinctly longer than carpus, telson slender, elongate, length >2X basal width, apex acute, simple . . . . . *G. calitemplado* Barnard
   Gnathopod propod shorter than carpus; telson shorter, apex tidentate . . . . . *G. liliuokilaniae* Barnard

almond-shaped, outer row of facets largest. Antenna 1 shorter than antenna 2, lacking accessory flagellum; peduncular segments short, flagellum 6-segmented. Antenna 2, flagellum 9-10 segmented.

Mandibular molar stout triturative; spine row with 7-8 slender blades; left lacinia ~8-dentate; palp segment 3 slender, shorter than segment 2, apex narrowly truncate, with 2-3 longish simple setae. Maxilla 1, outer plate oblique apex with 8 stout spine-teeth and proximal tuft of fine setae; palp stout, 1-segmented, with several apical setae. Maxilla 2, inner distal margin with several slender setae; outer plate stout, with 4 apical setae. Maxilliped, inner plate narrow, apex subtruncate; outer plate medium broad, with inner marginal subapical incision; palp segment 2 exceeding outer plate; segment 3 shorter than 2.

Coxa 1 narrow, rounded below; coxae medium deep, increasing posteriorly, smooth below. Gnathopods 1 & 2, propods small, subrectangular; palms short, oblique, convex, denticulate, not sharply demarcated at posterior angle; dactyls stout, pectinate behind, unguis overlapping palm. Gnathopod 1, carpal lobe very short, little produced. Gnathopod 2 larger, carpus shorter than propod, posterior lobe short, stiff-setose, extending about half length of propod.

Peraeopods 3 & 4 very slender, weakly armed; dactyls slender, medium long. Coxae 5-7 deeply posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 long, 5 short; dactyls slender, medium long .

Pleon side plate 3, lower margin straight, hind corner slightly produced. Pleopod rami 9-10 segmented, slightly longer than thick peduncle. Uropod 1 slender, rami subequal, margins spinose. Uropod 2, rami marginally short-spinose; outer ramus >1/2 inner. Uropod 3, rami much shorter than slender peduncle, marginally smooth, distinctly exceeding telson.

Telson narrowly subtriangular, apex tridentate

Brood plates 2-4 large; 5 small with 3-4 distal marginal setae.

**Etymology:** The species name recognizes the extensive contributions of Dr. Derek V. Ellis, University of Victoria, in the development and teaching of coastal marine ecological and environmental concepts.

**Distribution:** Only 7 specimens known; from shallow-sublittoral depths off southern Vancouver Island, B. C.

**Remarks:** *Gitana ellisi* is closest to *G. sarsii* Boeck; however, its larger eyes, more distinctly subchelate gnathopods with less produced carpal lobes, smaller coxal plates, and much less markedly reduced mandibular palp are more plesiomorphic character states than in *G. sarsi*.

### *Gitanopsis* Sars (restricted)

*Gitanopsis* Sars, 1895: 223;—Stebbing 1906: 153;—Gurjanova 1951: 302.
*Gitanopsis* Lincoln 1979: 164 (part);—Barnard 1962: 130 key (part);—Barnard & Karaman 1991: 97 (part).
non: *Gitanopsis* McKinney 1978: 140.—Karaman 1980: 44;—Hirayama 1983: 124.

**Type species:** *Amphilochus bispinosa* Boeck, 1871, original designation by G. O. Sars.

**Species:** *Gitanopsis inermis* Sars, 1883; *G. arctica* Sars, 1895;—Shoemaker 1955; *G. abyssicola* Sars, 1895; *Gitanopsis* sp. A, Just ,1980; *Gitanopsis* sp. B, Just, 1980.

## KEY TO NORTH PACIFIC SPECIES OF *HOURSTONIUS*

(*Gitanopsis iseebi* Yamato transferred to *Afrogitanopsis*)

1. Gnathopods 1 & 2, propods subsimilar in size and shape, palmar angle squared, defined by small tooth and spine; carpus, posterior lobe short, little produced ..... ***H. pusilloides*** (Shoemaker)
   Gnathopod 2 distinctly larger than gnathopod 1, palmar angle obtuse, defined by spine(s) only; carpus of gnathopod 2 strongly produced posterodistally below propod ..... 2.

2. Gnathopods 1 & 2, posterior angle of propod defined by single spine; maxilliped, outer plate markedly incised mediodistally; Hawaiian islands..... ***H. pele*** (Barnard)
   Gnathopod propods, posterior angle with paired spines; maxilliped, puter plate little or not incised mediodistally ..... 3.

3. Telson apically acute, minutely bifid; maxilliped palp, segment 2 distinctly longer than segment 3; mandibular spine row short, ~6-bladed ..... ***H. japonica*** (Hirayama)
   Telson, apex subacute or rounded; maxilliped palp segment 3 short, not longer than segment 3; mandibular spine row with 8-12 blades ..... 4.

4. Gnathopod 2, propod with two prominent anterior submarginal spines; gnathopod 1, anterior margin of basis setose throughout; maxilla 2, inner plate weak, little broader than outer ..... 5.
   Gnathopod 2 lacking anterior submarginal spines; gnathopod 1, anterior margin of basis nearly bare; maxilla 2, inner plate normal, setose, broader than outer plate ..... 6.

5. Gnathopod 2, carpal lobe elongate, extending almost to palmar angle; telson elongate, length >2X maximum width; N. American Pacific ..... ***H. vilordes*** (Barnard) (p. 11)
   Gnathopod 2, carpal lobe short, ~ 3/4 length of posterior margin of propod; telson short, length 1.5 X maximum width; Gulf of Mexico ..... ***H. laguna*** (McKinney)

6. Telson narrow, elongate, length > 2X maximum width; gnathopod 2, carpal lobe extending beyond posterior palmar angle ..... 7.
   Telson short, broader, length not > 2X width;gnathopod 2, carpal lobe not quite reaching posterior palmar angle ..... ***H. breviculus*** (Hirayama).

7. Abdominal (epimeral) side plate 3, hind corner slightly produced; uropod 2, outer ramus normal , >1/2 length of inner ramus ..... ***H. robastodentes*** (Hirayama)
   Epimeral plate 3, hind corner squared or rounded; uropod 2 outer ramus short, not greater than 1/2 length of outer ramus ..... ***H. longus*** (Hirayama)

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**Diagnosis**: Rostrum medium; anterior head margin usually acute; eye round. Antennae usually subequal in length; accessory flagellum lacking or very minute.

Upper lip shallowly notched, lobes subsymmetrical. Lower lip, inner margins strongly notched. Mandible: molar process large, triturating surface without raised marginal spines; spine row with few blades; palp segment 3 elongate, setulose near apex. Maxilla 1 normal, palp 2-segmented. Maxilla 2 normal, inner plate narrow. Maxilliped palp slender, segment 2 often short.

Coxae 2-4 large, lower margin weakly serrate. Gnathopods 1 & 2 medium to weakly subchelate; prododal palm not demarcated from posterior margin; carpus of medium length, lobe produced. Peraepods 3 & 4, dactyls slender, medium. Coxae 5-7 regularly posterolobate. Peraeopods 5-7, dactyls slender, medium long.

Epimeral plate 3, hind corner subquadrate . Uropod 3 relatively short, little exceeding uropod 1. Telson elongate, narrowing, apex acute, minutely tridentate.

**Distribution**: Holarctic and northern North Atlantic, 0 -875 m. in depth.

**Remarks:** *Gitanopsis* sens. lat. (e.g., Barnard & Karaman, loc. cit.) here consists of three groups: *Gitanopsis* Boeck sens. str. (Arctic and northern North Atlantic in distribution); and *Hourstonius* new genus, mainly in

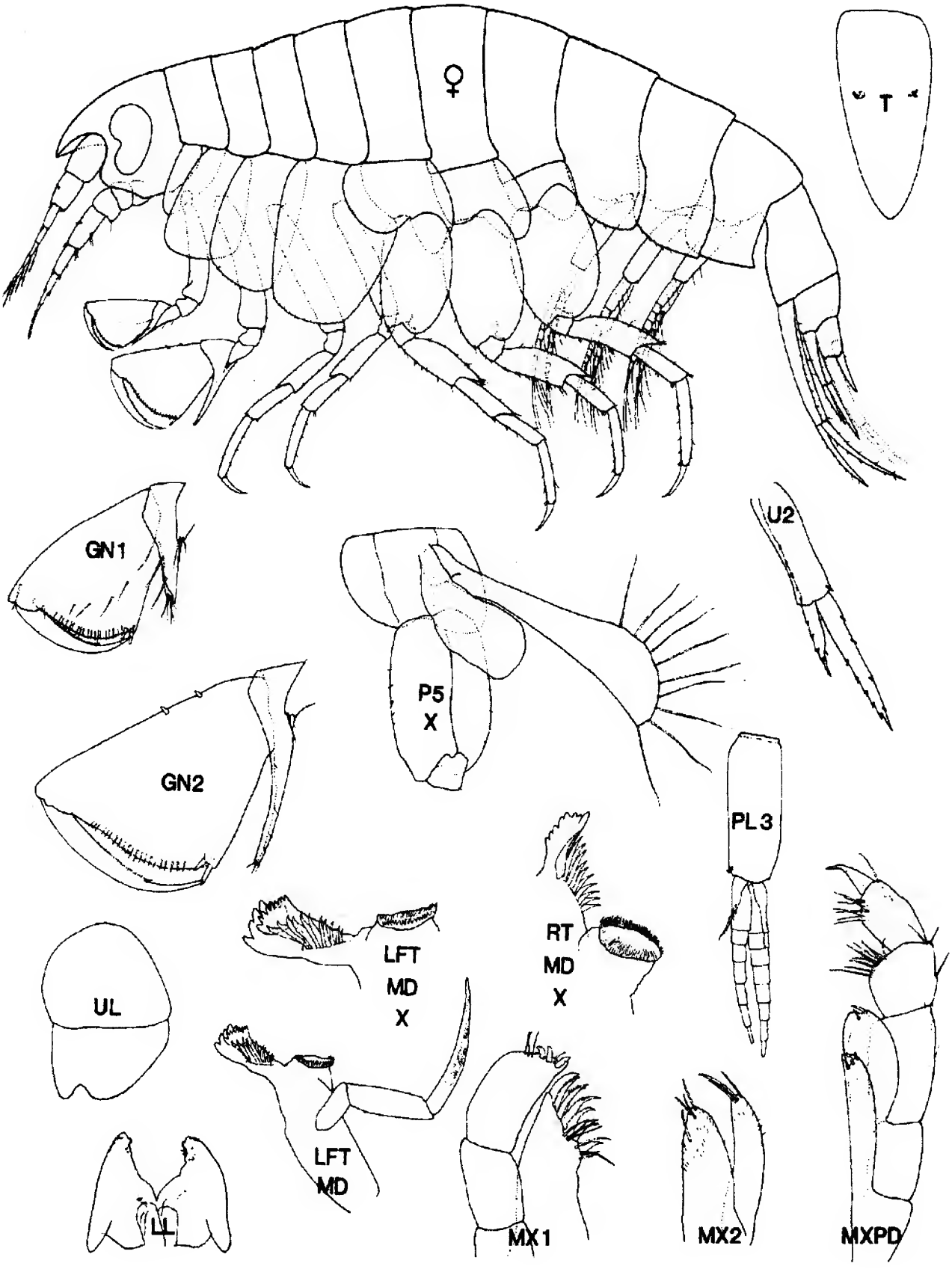


Fig. 3. ***Hourstonius vilordes*** ( Barnard). ♀ ov. (3..9 mm). Hinks I., N. end Aristazabel I., B .C.

the North Pacific region, with some species in the Gulf of Mexico, and possibly coastal waters of the African South Atlantic region. A third generic group, informally recognizable and yet unnamed within *Gitanopsis* (sens. lat.), may be represented by *G. marionis* (Stebbing, 1888), as figured by Bellan-Santini & Ledoyer (1974), *G. tai* Myers, 1985, and several other largely Indo-Pacific and southern hemispheric species (except *G. squamosa* (Thompson, 1880) as listed by Barnard & Karaman (1991).

Principal characters and character states utilized in keys, diagnoses, and numerical analyses pertaining to the genus *Gitanopsis* (sens. lat.) are represented in Fig. 1 (p. 55).

### *Hourstonius*, new genus

*Gitanopsis* Sars, 1895: 224 (part);— Barnard 1962: 130 (key, part);—Hirayama 1983: 124 (key);—Barnard & Karaman 1991: 97 (part);—Ishimaru, 1994: 52 (species list).
non *Gitanopsis* Gurjanova 1951: 302;—Lincoln 1979: 164.

**Type species:** *Gitanopsis vilordes* J. L. Barnard, 1962

**Species:** *Hourstonius breviculus* (Hirayama, 1983); *H. japonica* (Hirayama, 1983); *H. longus* (Hirayama, 1983); *H. robastodentes* (Hirayama, 1983) (Japan); *H. laguna* (McKinney, 1978); *H. tortugae* (Shoemaker 1942)(Florida); *H. pusilloides* (Shoemaker, 1933; *H. pusilla* (K. H. Barnard, 1916)(S. Africa); *H. pele* (J. L. Barnard, 1970); *H. baciroa* (J. L. Barnard, 1979) (Galapagos); *H. magdai* (Reid, 1951)(Trop. Atlantic) non: *Afrogitanopsis paguri* (Myers, 1974) (W. Indian); *A. iseebi* (Yamato, 1993)(Japan).

**Diagnosis:** Anterior head lobe generally rounded. Accessory flagellum 1-segmented or minute.

Upper lip notched, lobes asymmetrical; lower lip, inner marginal "notch" weak or lacking; mandible, molar distinct, outer triturating ridge with raised spines; maxilla 1, palp slightly modified; maxilliped, palp segment 3 short; coxa 2, lower margin smooth (not serrate); gnathopods 1 & 2 strongly subchelate, propod with paired spines at posterodistal angle demarcating palm; gnathopod 2, carpus narrow, posterior lobe elongate;

Epimeral plate 3, hind corner squared or rounded; telson linguiform, medium to long, apex broadly or sharply rounded (acute in *H. japonica*).

**Distribution:** Mainly North Pacific, with some species in the Gulf of Mexico, and possibly coastal waters of the African South Atlantic region.

**Etymology:** The genus is named in honour of the late Alan S. Hourston, fisheries scientist with the Pacific Biological Station, Nanaimo, British Columbia. Dr. Hourston, his wife Barbara, and their family provided much help and encouragement to the senior author and his family during the 25-year period of field work for the Pacific amphipod program, 1955-1980.

**Remarks:** Members of this genus are readily distinguished from species of *Gitanopsis* Sars (sens. str.) in possessing an accessory flagellum, more strongly subchelate gnathopods with shorter carpus; weakly (or not) serrated lower margin of coxa 2; and linguiform telson with rounded apex. Moreover, species of *Gitanopsis* (sens. str.) are mainly Arctic and North Atlantic in distribution.

Members of the third generic group (*G. marionis, G. squamosa, G. tai*, and several others (see *Gitanopsis* above). Members appear superficially more closely similar in some character states (e.g., of accessory flagellum, upper lip) to *Hourstonius* than to *Gitanopsis* sens. str., but detailed analysis is beyond the scope of the present study.

### *Hourstonius vilordes* (J. L. Barnard, 1962) (Fig. 3)

*Gitanopsis vilordes* Barnard, 1962: 131, fig. 6;—1969b: 82;—1975: 344, fig. 190;—Austin, 1985: 593;—Staude, 1987: 379.

**Material Examined:**

**ALASKA**

**SE Alaska, ELB Stns., 1961:**

A3, Little Daykoo, Dall I. (54°42'N, 132° 42' W); MW-LW, May 31 - 2 ♀♀, NMCC1992-0215.

**BRITISH COLUMBIA.**

**Queen Charlotte Islands, ELB Stns., 1957:**

W4b, Small bay, north shore Hippa Passage (53°27'N, 132° 58'W), 6-10 m dredge, gravel, stones, shells, Aug. 10. - 1 ♀, NMCC1992-0204.

**North Central coast, ELB Stns., 1964:**

H3, Cockle Bay, Lady Douglas I. (52°21'N, 128°23'W), sand, *Zostera*, kelp, LW, July 9. - 4 ♀♀, NMCC1992-0219.
H5, Hinks I., north end Aristazabal I. (52°38'N, 129°05' W), stones, Phyllosp[adix, kelp LW, July 10.- ♀ (ov.) (**Fig'd specimen**), 2 ♀♀; 3 ♂♂, 57 imm.; slide mounts: ♀♀ (1.8mm,

2.2 mm, 2.3 mm, 2.4 mm. 2.4 mm, 2.6 mm, 2.7 mm, 2. 9 mm), NMCC1992-0220. H26, Cox Pt., inlet at mouth (53°08'N, 129°45'W), shelly sand, kelp, LW, July 19. - 2 ♀♀, NMCC1992-0225. H65, Christie Pass, cove on south side Hurst I. (50°50'N, 127°35'W), shelly gravel, kelp, MW-LW, Aug. 11. - 8 ♀♀, NMCC1992-0232.

**Northern Vancouver I., ELB Stns., 1959:**

O4, Browning Inlet (50°30'N, 128°06'W), shelly sand, eel grass, LW, July 19. - 1 ♀, NMCC1992- 0213? V5, Lemon Pt., Nigei I. (50°51'N, 127°46'W), *Phyllospadix, Corallina*, fucoids, LW, Aug. 7. - 1 ♀, NMCC1992-0210. V7, Lady Ellen Pt.,Broughton Str. (50°36'N, 127°07'W) - 1 ♀, NMCC1992-0211. V10, Alert Bay, Broughton Str. (50°35'N, 126°56'W) muddy sand, kelp, LW, Aug. 1 - 1 ♀, NMCC1992-0212. V17, Boat Bay, Cracroft I. (50°31'N, 126°34'W), coarse sand, eelgrass, LW, Aug. 5. - 3 ♀♀, NMCC1992-0217. V20, Brown Bay (50°10'N, 125°22'W), coarse sand, kelp, LW, June 22. - 1 ♂, 2 ♀♀, NMCC1992-0214. N11, Port Progress, Queen Charlotte Str. (50°55'N, 127°16' W), sandy mud, *Zostera*, LW, Aug. 4 - 3♀♀, NMCC1992-0205.

**Southern Vancouver Island, ELB Stns., 1955:**

F6, Telegraph Bay (48°27'N, 123°17'W) - 1 ♀ NMCC1992-0202. Victoria region (48°N, 123°W), KEC Stn.?, 1981. - 1 ♀, NMCC1992- 0249; Ibid., - 3 ♂♂, 1 ♀ ov. (2.5 mm), slide mount, 10 females, NMCC1992-0250; Ibid., - 1♀, NMCC1992-0251.

**Diagnosis:** Female ov. (3.9 mm) (fig'd specimen).

Rostrum medium. Eye large, subreniform. Antennae short, subequal. Antenna 1, flagellum 5-6 segmented; accessory flagellum minute. Antenna 2, flagellum 6-segmented.

Upper lip, apex distinctly asymmetrical. Lower lip with weak inner "shoulders". Left mandible, lacinia 8-9 cuspate; spine row with 10-12 slender blades; palp segment 3 distinctly longer than 2, inner distal margin finely pectinate, apex sharply acute.. Maxilla 1, inner plate with 7 apical spine teeth and 4-5 inner apical seta; palp and segments stout. Maxilla 2, plate medium, weakly armed. Maxilliped, plates narrow; palp segment 1 large, length nearly equal to 2 & 3 combined.

Coxa 1 narrow elongate; coxae 2 -4 large deep, smooth below. Gnathopods 1 & 2 propods large, palms smoothly convex, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyls slender, finely pectinate behind except on unguis. Gnathopod 1, carpal lobe spinose, produced 2/3 length of posterior margin of propod. Gnathopod 2, carpus narrow, lobe extending almost to posterior angle of propod.

Peraeopods 3 & 4 slender, weakly armed; dactyls slender. Coxae 5-7 normally posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally homopodous; bases regularly expanded, posteriorly slightly increasing in size; dactyls slender, medium long .

Pleon side plates 2 &3, hind corners weakly acuminate. Pleopod rami slightly longer than peduncle, 7-8 segmented. Uropod 1, rami markedly unequal, margins weakly spinose. Uropod 2, ramus marginally short-spinose; outer ramus ~= 1/2 inner. Uropod 3, rami short, broad, marginally smooth, slightly exceeding telson.

Telson elongate, smooth, apex narrowly rounded.

Brood plates medium broad; plate 5 with 10-12 distal marginal setae.

**Distribution:** Shallow littoral depths from SE Alaska to southern Vancouver Island, south to central and southern California.

**Remarks:** In character state similarity, *Hourstonius vilordes* appears somewhat closer to species of *Hourstonius* from the Gulf of Mexico than to species of "Gitanopsis" (sens. lat.) described by Hirayama (1983) from Japanese coastal marine waters (see key to species, p. 9). *H. vilordes* differs from the Hawaiian species, *H. pele* (Barnard, 1970), in its larger coxal plate 2, larger mandibular palp, and narrower telson, as well as character states of the gnathopods given in the key.

### *Amphilochus* Bate (restricted)

*Amphilochus* Bate, 1862: 107.—Stebbing 1906: 149 (part);—Lincoln 1979: 148 (part);—Krapp-Schickel 1982: 74 (part);—Barnard & Karaman 1991: 96 (part).

**Type species.** *Amphilochus manudens* Bate, 1862, monotypy.

**Species**: *Amphilochus tenuimanus* Boeck, 1871; *A. planierensis* Ledoyer, 1977.

**Diagnosis:** Rostrum medium; anterior head lobe acute; eyes rounded. Antennae subequal in length; accessory flagellum lacking or minute.

Upper lip, apical incision shallow, lobes sub-symmetrical. Lower lip, inner margins smooth. Mandible: molar very reduced, knob-like, lacking triturating ridges; spine-row medium; palp segment 3 elongate. Maxilla 1 normal, palp 2-segmented. Maxilla 2 regular, outer plate slender. Maxilliped palp slender.

Coxal plates 2-4 large, lower margins serrate. Gnathopods 1 & 2 medium to strongly subchelate, palmar

## KEY TO NORTHERN PACIFIC AND ATLANTIC SPECIES OF *APOLOCHUS*

(see character states of subgroups 1 & 2 of Fig. 4, p. 64 )

1. Mandibular molar small, knob-like, lacking triturating ridges; maxilla 2, plates reduced, weakly armed; peraeopods 3 & 4, dactyls short, thick (North American Pacific subgroup). . . . . 2.
Mandibular molar distinct, apex acute with few triturating ridges, or flat, with several ridges; maxilla 2, inner plate broad; peraeopods 3 & 4, dactyls usually slender, medium (Atlantic-Mediterranean regional subgroup). . . . . 4.

2. Gnathopod 2, carpal lobe short, <1/2 propod margin; mandibular spine-row 10-12 bladed; uropod 2, rami nearly bare; telson elongate, 2 1/2X width . . . . . ***A. litoralis*** (Stout) (p. 16)
Gnathopod 2, carpal lobe long, reaching posterior palmar angle; mandibular spine row long, 14-16 bladed; uropod 2, rami marginally spinose; telson shorter, length 2X width . . . . . 3.

3. Antenna 1 shorter than 2; gnathopod 2, palm shallowly convex, nearly perpendicular; maxilliped outer plate wide, little longer than broad . . . . . ***A. barnardi*, n. sp.** (p. 18 )
Antennae 1 & 2 short, subequal in length; gnathopod 2, palm strongly convex, oblique; maxilliped, outer plate medium, longer than wide . . . . . ***A. staudei*, n. sp.** (p. 19 )

4.. Mandibular molar elongate, apex subacute, with few (or no) triturating ridges; gnathopod 2, carpus short, < 1/3 anterior margin of propod . . . . . 5.
Mandibular molar short, apex sub truncate, flat, with several triturating ridges; gnathopod 2, carpus medium, length > 1/ 3 anterior margin of propod. . . . . 7.

5. Gnathopod 2 , propod large, carpal lobe extending almost to palmar angle; accessory flagellum very minute or lacking . . . . . ***A. picadurus*** (J. L. Barnard )
Gnathopod 2, propod medium to small, carpal lobe extending little more than half way to palmar angle; accessory flagellum distinct, 1-segmented . . . . . 6.

6. Uropod 3, rami subequal; maxilliped, outer plate broader than long . . . . . ***A. borealis*** (Enequist)
Uropod 3, inner ramus distinctly longer than outer ramus; maxilliped outer plate longer than broad. . . . . ***A. pillaii*** (Barnard & Thomas)

7. Antennae subequal in length; coxa 1 serrate below; mandibular spine-row with 8-10 blades . . . . . 8.
Antenna 1 short flagellum little beyond peduncle of A2; coxa 2 smooth below; mandibular spine row with ~14 blades . . . . . ***A. neopolitanus*** complex, N-E. Atlantic 9.

8. Gnathopod 2, propod with 4 stout antero-marginal spines . . . . . ***A. casahoya*** (McKinney)
Gnathopod 2, propod with 2 stout antero-marginal spines . . . . . ***A. delacaya*** (McKinney)

9. Uropod 2, ramal margins spinose; coxa 1 subrectangular, lower margin smooth; telson short, length 1.5 X maximum width . . . . . ***A. neopolitanus*** (Della Valle) (fide Krapp-Schickel)*
Uropod 2, margins of rami nearly unarmed; coxa 1 subtriangular, lower margin with distinct notch; telson regular, length about twice width . . **Apolochus** sp. (= *A. picadurus* Krapp-Schickel, 1982).

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margin not demarcated from posterior margin by paired spines; carpus medium, lobe variously produced; dactyls finely denticulate. Peraeopods 3-4, dactyls slender, medium long. Coxae 5-7 deep, shallowly posterolobate. Peraeopods 5-7, dactyls slender, medium long.

Pleon segment 3, hind corner with small cusp. Pleopods regular. Uropod 3, inner ramus slightly broadened. Telson elongate, narrowing distally, apex acute, minutely dentate.

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* "*Amphilochus*" *neopolitanus* of Lincoln (1979) differs from that of Krapp-Schickel (1982)

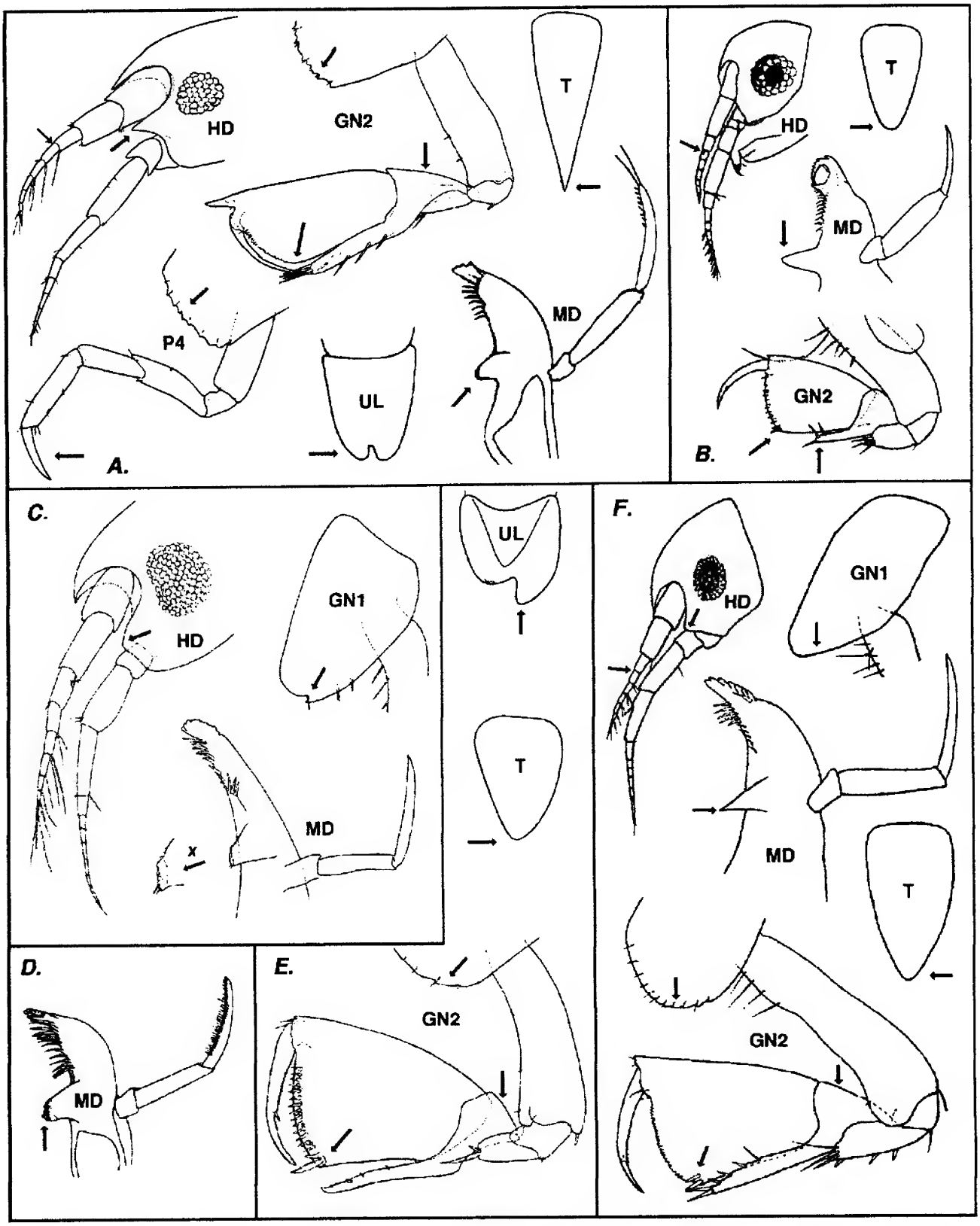



Fig. 4. Selected Characters and Character States within ***Amphilochus*** and ***Apolochus***. A. ***Amphilochus manudens*** Bate [modifed from Lincoln (1979), Sars (1895)]; B. ***Apolochus borealis*** (Enequist, 1950); C. ***Apolochus*** sp. [= *A. picadurus* (Krapp-Schickel (1982)]; D. ***Apolochus delacaya*** (McKinney, 1978). E. ***Apolochus neopolitanus*** Della Valle (after Krapp-Schickel (1982)]; F. ***Apolochus picadurus*** (Barnard, 1962). **[see p. 28 for figure legend]**

**Distribution:** Northern North Atlantic, N. American [Brunel et al. 1998) and boreal European-Mediterranean region.

**Habitat:** On scleractinian and horny corals, 0-600 m.

**Remarks:** *Amphilochus* Bate (sens. str.) is defined by: anterior head lobe acute; accessory flagellum lacking; upper lip apical lobes subsymmetrical; gnathopod propods lacking posterodistal palmar spines; coxae 2-4 with serrate lower margins; peraeopod dactyls elongate; and telson apically acute, minutely tridentate.

The form of the gnathopods, mouthparts, and telson suggest that *Amphilochus* sens. str. may have been para-ancestral to regionally more advanced genera such as *Amphilochoides* Sars, 1895, and *Paramphilochoides* Lincoln, 1979. However, these latter two genera may themselves require redefinition. Thus, the type species of *Amphilochoides* [*A. boecki* Sars (= *A. odontonyx* Sars, 1895)] possesses a unique combination of generic-level character states: upper lip, apical lobes subsymmetrical; maxilla 2 plates small, partly fused; dactyls of both gnathopod 1 & gnathopod 2 with proximal nodiform process; and epimeral plate 3, hind corner toothed. At least three species with normally reduced mandibular molar, presently included in the genus *Amphilochoides* by Barnard & Karaman (1991), differ in the above character states. Thus, "*Amphilochoides" longimanus* Chevreux, 1888, *A. serratipes* Norman, 1869, and a distinctive Mediterranean species figured as *A. serratipes* by Krapp-Schickel (1982) might justify separate generic recognition.

Despite aberrencies in the form of the gnathopods, in overall character-state similarity the genus *Paramphilochus* Ishimaru & Ikehara, 1986, appears more closely similar to Pacific members of *Apolochus* and *Hourstonius* than to *Amphilochus* (sens. str.).

**Apolochus,** new genus

*Amphilochus* Sars 1895: 215 (part); Stebbing 1906: 149(part);—Barnard 1969a: 136(part);—Lincoln 1979: 148 (part);—Krapp-Schickel 1982: 74 (part); Barnard & Karaman 1991: 96 (part).
non: *Amphilochus* Bate, 1862: 107.

**Type species**: *Amphilochus neopolitanus* Della Valle, 1893.

**Species:** 1. Nominate subgroup: *Apolochus picadurus* (Barnard, 1962) (California); *Apolochus* species (= *A. picadurus* Krapp-Schickel, 1982) (Mediterranean); *A. borealis* (Enequist, 1950) (NW Europe); *A. pillaii* (Barnard & Thomas, 1983) (Florida); *A. casahoya* (McKinney, 1978) (Gulf of Mexico); *A. delacaya* (McKinney, 1978) (Gulf of Mexico); *A. kailua* Barnard, 1970 (Hawaii); *A. likelike* Barnard, 1970 (Hawaii); *A. menehune* Barnard, 1970 (Hawaii).
2. Eastern Pacific subgroup: *Apolochus litoralis* (Stout, 1912) (p. 16); *A. barnardi*, new species (p. 18); *A. staudei*, new species (p. 19).
3. Mediterranean "southern" subgroup: *Apolochus brunneus* (Della Valle, 1893), *A. spencebatei* (Stebbing, 1876), and two species described from the Indian Ocean region as *Amphilochus neopolitanus* by Ledoyer 1978, 1979.

**Diagnosis:** Anterior head lobe rounded. Antenna 1 short to medium, peduncular segments 1 & 2 slightly broadened posteriorly; accessory flagellum 1-segmented, rarely lacking.

Upper lip, apical lobes asymmetrical. Lower lip, inner margins variously "notched". Mandible, molar reduced, apically with few triturating ridges, setae, or none; spine-row well developed; palp segment 3 little longer than segment 2. Maxilla 1, outer plate spines regular; palp segment 1 enlarged. Maxilla 2, setation of plates tending to reduction. Maxilliped outer plate broad, palp regular.

Coxae 2-4 weakly or not serrate below. Gnathopod 2, carpus short to medium in length, posterior lobe well developed; palmar margin of propod distinct, steeply oblique or nearly vertical, palmar angle defined by 1-2 spines. Peraeopods 3 & 4, dactyls short to medium, shorter than those of peraeopods 5-7.

Telson linguiform, apex sharply rounded or subacute. Brood plate (P5) short, with 5-6 marginal setae.

**Etymology:** A combining form of "apo" and "lochus", referring to the generally advanced nature of the character states of the genus.

**Remarks:** The genus *Amphilochus* Bate, 1862 (sens. lat.), previously encompassed a heterogeneous group of amphilochid species characterized by stoutly subchelate gnathopods and reduced, essentially non-triturative, mandibular molar process. Characters and character states previously utilized in diagnoses and keys (above) have been limited in number and kind, and apparently not previously ordered or subject to numerical analysis.

A semi-phyletic phenogram of northern hemisphere

species of *Amphilochus* (sens. lat.) (see p. 9, supporting data supplied on request) suggests that the name *Amphilochus* is more realistically confined to the type species *Amphilochus manudens* Bate, 1862, *A. tenuimanus* Boeck, 1871, and (less closely) *A. planierensis* Ledoyer, 1977.

### *Apolochus litoralis* (Stout)
(Fig . 5)

*Amphilochus litoralis* Stout, 1912: 136, fig. 78;—Barnard 1962: 82;—Barnard 1969b: 124, fig.2;—Barnard 1975: 358, fig. 327;—Staude 1987: 379;—Barnard & Karaman 1991: 96.

**Material Examined:** 32 lots of specimens containing about 80 specimens (mostly ovig. females but also incl. 6 males and a few imm.), mostly from high salinity outer coast stations, from about Sitka, SE Alaska. south ward through the Queen Charlottes Islands,the north-central B. C. coast, Vancouver I.,Washington state, to southern California.

**ALASKA**

**SE Alaska, ELB Stns.,**

**1961:**

A168, Klokachef I., Chickagof I. (57°25'N, 135°52'W), kelp over boulders, LW, July 24. - ♀ ov. (damaged), NMCC-1992-0217. A175, West Eugenia Pt., San Juan Batista I. (55°26.44'N, 133°17.18'W), *Zostera*, algae, sand, rock, LW, July 26. - 1♂, 1 ♀, NMCC1992-0218.

**1980:**

S5B1, N.W. end Hogan I., west cove (57°43'N, 136°15.5'W) prganic debris, slatey gravel, LW July 28. - 1 ♀, NMCC1992-0245. S23F1, Taigud I., south beach, Baranof I. (56°54.5'N, 135°24'W), kelp, sand, LW, Aug. 4. - 3 ♀♀ + 2 ♀♀ (damaged), NMCC1992-0247.

**BRITISH COLUMBIA**

**Queen Charlotte Ids., ELB Stns., 1957:**

H2, Parry Passage, E. of Kiusta (54°10'N, 133°01'W), *Phyllospadix*, kelp, over coarse sand, LW, Aug. 24. - 1 ♀, NMCC-1992-0203.

**Northcentral coast, ELB Stns., 1964:**

H5, Hinks I., N. end Aristazabel I. (52°38'N, 129°05'W), *Phyllospadix*, kelp, LW, July 9. - 1 ♀, NMCC-1992-0220. H20, McCauley I., N. end (53°43'N, 130°15'W), fine sand, LW, July 17. - 2 ♀♀, NMCC1992-0221. H47, Codfish Passage, Miles I. (52°05'N, 128°19'W), *Zostera*, kelp, algal mats, coarse shelly sand, LW, Aug. 5- 1 ♂, 5 ♀♀, NMCC-1992-0221. H50, Goose I. South beach (51°57'N, 128°26'W), *Zostera*, algae, fine shell, sand, Aug. 6. - 1 ♀, NMCC1992-0229. H57, cove off Nolan Pass, S. end Hunter I. (51°43'N, 128°05'W), shells, gravel, mud, LW, Aug. 8. - 2 ♀♀, NMCC1992-0231. H65, Christie Pass, cove on S. side Hurst I. (50°50'N 127°36'W), kelp, shelly gravel, LW, Aug 11. - 1 ♀, NMCC1992-0232.

**Northern Vancouver I., ELB Stns., 1959:**

O3, Grant Bay, Quatsino Sound (50°28'N, 128°05'W), coarse shelly sand, LW, July 18. - 3♀♀, NMCC1992-0209. O11, Hesquiat, at Matlakaw Pt. (49°23'N, 126°28'W), *Phyllospadix*, kelp, over gravel -1 ♀,NMCC1992-0208. N11,Port Progress (50° 55'N, 127°16'W), *Zostera* over sandy mud, stones, LW, Aug. 4. - 1♀, NMCC1992-0205. V5, Lemon Pt., Nigei I. (50°51'N, 127°46'W), *Phyllospadix*, fucoids, *Corallina*, over stones, LW. - 6♀♀, NMCC-1992-0210. V4b, Roller Bay, Hope I. (50°56'N, 127°56'W), *Phyllospadix*, kelp, coarse sand, LW, July 22. - 3♀♀. NMCC1992-0209.

**Southern Vancouver I., ELB Stns.**

**1955:** F1 Wiffen Spit, Sooke (48°21'N, 123°45'W), algae on gravel, stones, LW - 4 ♀♀ , NMCC1992-0201.

**1970:** P718, Becher Bay at Head (48°21'N, 123°35'W), algae on stones, gravel, LW, July 31 - 1♀, NMCC1992-0234.

**1977:** B6a, Trial Island Pt., Victoria (48°24'N, 123°19'W) - 1 ♀, NMCC 1977-181.

**1980:** Deer I., Victoria region (50.6°N, 127.9°W?) - 2 ♀♀, NMCC1992-0244.

**1981**: Victoria region (48°N, 123°W), KEC Stn.?- 4 ♀♀, NMCC1992-0234?; Ibid. - 1 ♂, 3♀♀, NMCC1992-0248; Ibid. - 1♂, 1♀, NMCC1992-0249; Ibid.- 4♂♂, 1♀, NMCC1992-0251.

**Vancouver I., outer coast, ELB Stns.**

**1976:**

B4, off Brady's Beach, Bamfield (48°50.03'N,125°08'W), sand, algae, 60-70 m dredge, June 25 - 2 ♀♀, NMCC1992-0235. B5, Brady's Beach, S. side (48°49.08' N, 125°08' W), *Phyllospadix*, kelp, fucoids, on sand and rock, LW. - 3 ♀♀, NMCC1992-0236. B7, Broken Islands, W. side of Wouwer I. (48°51.6'N, 125°21'W)Phyllospadix, kelp, on bedrock, LW. - 1 ♀, NMCC1992-0237.

**1977:**

B8, off Brady's Beach, Bamfield (48°49.6'N, 125°09.2'W), sand and algae, 5-10 m dredge, May 21. - 3 ♀♀, 2 imm, NMCC1992-0239. B13, Trevor Channel, off Brady's Beach (48°52'N 125°08'W), hard sand algae, 6-14 m dredge, May 25. - 1♀, NMCC1992- 0290. B14, Trevor Channel off Execution Rock (48°48'N, 125°11.2'W), sandy mud, algae, 44-54 m dredge, May 25. - 1 ♀, NMCC1992-0241. B21b, off Brady's Beach, Bamfield (48°49.6'N, 125°09.2'W). sand, algae, 10-20 m dredge, June 1. - ♀ (2.8 mm) (**fig'd specimen**);10 ♀♀, NMCC1992-0242.

**US MAINLAND**

**Washington-Oregon, ELB Stns., 1966:**

W36, Clallam Bay, WA, at river mouth (48°15'N, 124°16'W), fine organic sand, *Phyllospadix, Chorda*, LW - 1 ♀, NMCC-1992-0233.

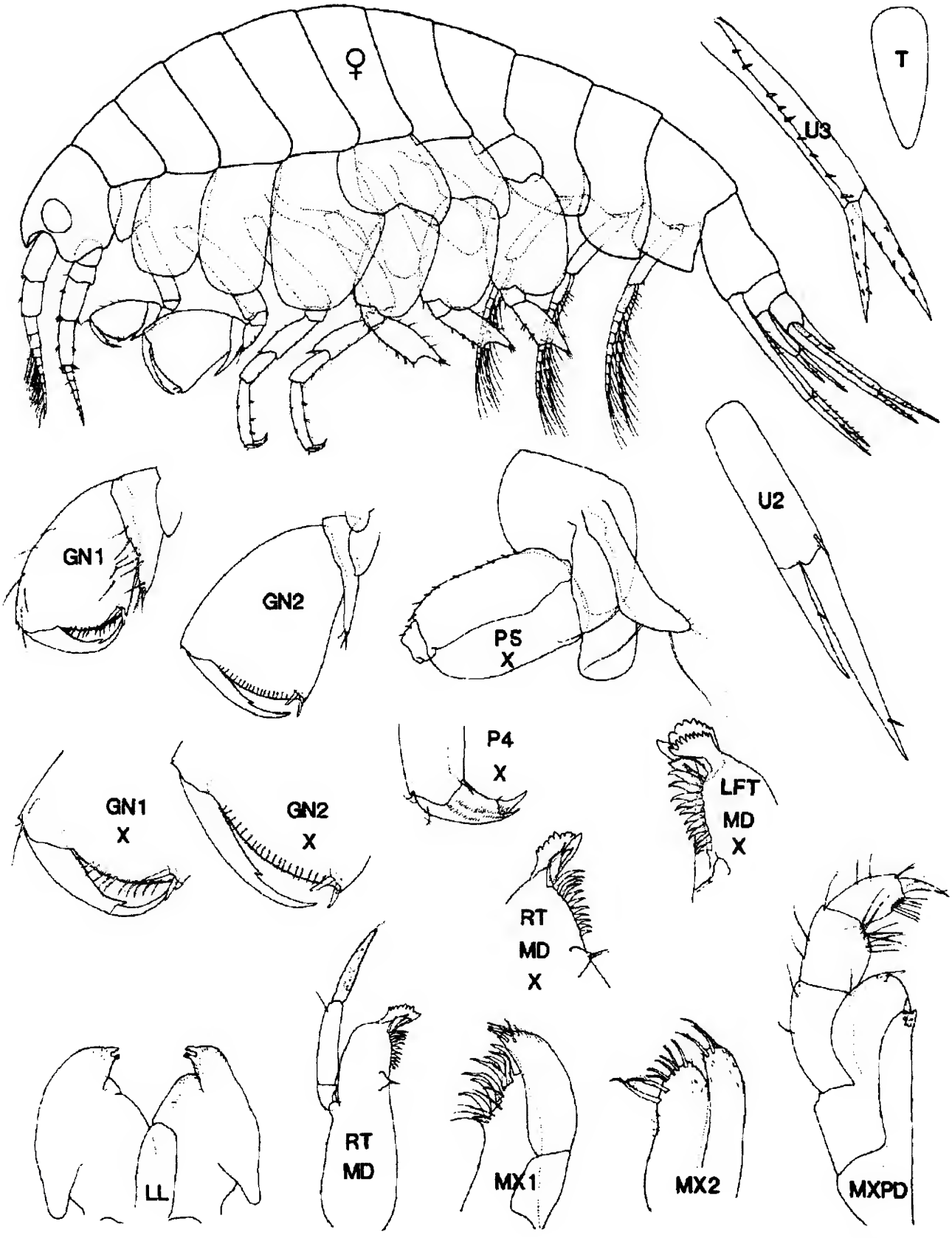



Fig. 5. ***Apolochus litoralis*** (Stout). Female ov. (2.8 mm). Off Brady's Beach, Vancouver I., B. C.

**Diagnosis:** Female ov. (4.0 mm) (fig'd specimen).

Rostrum strong, apex little deflexed. Eye medium, nearly round. Antennae short, subequal, flagella 7-8 segmented; accessory flagellum 1-segmented.

Mandible: molar a small triangular knob, apex with two setae; left mandible, lacinia 9-10 cuspate; incisor 9-dentate; spine row with 10-12 slender blades, stoutest distally; palp segment 3 little longer than 2, inner margin finely pectinate, apex blunt, with single short seta. Maxilla 1, inner plate, apex oblique, with 7 curved spine-teeth and 4-5 setae at inner angle; palp stout, segment 1 large. Maxilla 2, plates medium, inner plate with 8 apical setae. Maxilliped, inner plate narrow, apex subtruncate; outer plate broad inner margin smooth; palp segment 1 large, segment 2 extending considerably beyond outer plate.

Coxa 1 short, little concealed by coxa 2; coxae 2-4 large, deep, smoothly rounded below. Gnathopods 1 & 2 strongly subchelate. Gnathopod 1 much smaller; propod, palmar margin convex; oblique; dactyl stout, smooth behind, unguis medium; carpus short, posterior lobe short, anteriorly spinose-setose. Gnathopod 2, propod large, expanding distally, palm shallowly convex, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl stout, smooth behind, unguis medium; carpus short, posterior lobe short, nearly base, produced 1/3 length of posterior margin of propod.

Peraeopods 3 & 4 ordinary, posterior margin of segment 6 with 3 spines; dactyls short. Coxae 5-7 normally posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; dactyls short.

Pleon side plate 2 convex below, 3 nearly straight, corners not produced. Pleopod rami long, 9-10 segmented. Uropod 1, rami subequal, margins weakly spinose. Uropod 2, rami slender, nearly bare, outer ramus > 1/2 inner. Uropod 3 elongate, rami unequal, marginally spinose, greatly exceeding telson. Telson smooth, length about twice width, apex narrowly rounded.

Brood plates medium broad; 5 with 2-3 distal marginal setae.

**Distribution:** Intertidal and LW habitats, from southern California, north through Oregon, Washington, and B. C. to southern S.E. Alaska,

**Taxonomic Commentary:** As indicated in the key, *Amphilochus litoralis* and other American Pacific coast species are distinct from North Atlantic and Gulf species .

### *Apolochus barnardi* new species
(Fig. 6 )

*Amphilochus ?neopolitanus* cf. Della Valle fide Barnard, 1962: 126;—Barnard 1964: 105(?)—Barnard 1969b: 82.

**Material Examined:** None.

**Diagnosis** (partly after Barnard 1962): Female ov. (2.5 mm): Rostrum medium. Eye medium, narrowly subovate. Antennae medium short, subequal. Antenna 1, peduncular segments 1 & 2 short and deep, 2 with posterodistal tuft of setae; 3 small, narrow; flagellum 8-9 segmented; accessory flagellum minute. Antenna 2, flagellum 9-10 segmented.

Mandibular molar small, broadly triangular. Left mandible, lacinia 8-9 cuspate; spine row with 15-17 slender blades, distinctly largest distally; incisor multidentate; palp segment slightly longer than 2, inner margin finely pectinate, apex with single short seta. Maxilla 1, apical margin of inner plate nearly vertical, with 7 spine-teeth and 6-8 setae at inner angle; palp segments stout, segment 1 large. Maxilla 2, plates medium, inner plate with 6 marginal setae, proximally plumulose. Maxilliped, inner plates tall, narrow, apex subtruncate; outer plate short, broad, distal margin with several setae and stout spine, inner margin smooth; palp segment 2 distinctly exceeding outer plate; segment 3, inner distal margin with narrow denticles.

Coxa 1 short, little occluded by 2; coxae 2 -4 successively deepening, rounded below. Gnathopods 1 & 2 distinctly subchelate. Gnathopod 1, propod slightly expanding distally, palm convex, oblique; dactyl slender body denticulate behind, unguis elongate, slightly exceeding palmar angle; carpus narrow, lobe medium, extending about 1/2 posterior margin of propod. Gnathopod 2, propod large, broadening distally, palm convex, finely crenulate, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl slender, body finely pectinate behind, unguis elongate slightly exceeding palm; carpus short, posterior lobe elongate extending length of posterior margin of propod.

Peraeopods 3 & 4 medium, segment 6 with 4 posterior marginal spines; dactyls short, unguis short. Coxae 5-7 normally posterolobate, hind lobes rounded below, posteroventral margin of 7 weakly spinose. Peraeo-

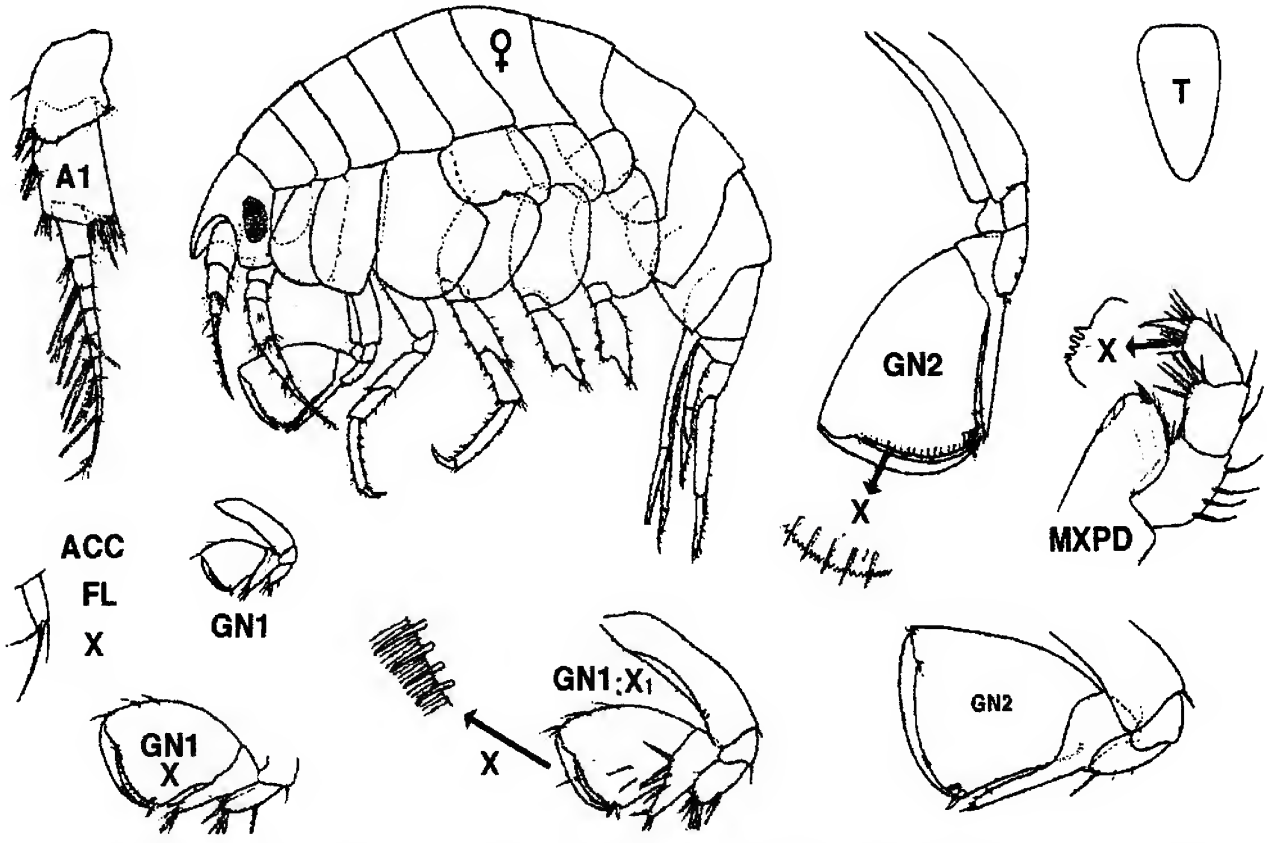



Fig. 6. ***Apolochus barnardi,*** new species (=*A. neopolitanus* cf. Della Valle fide J. L. Barnard,1962) (modified from Barnard, 1962).

pods 5-7 regularly homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; distal segments marginally spinose, esp. anteriorly; dactyls short.

Pleon side plates 2 & 3 convex below, hind corners not acuminate. Pleopod rami distinctly longer than peduncle, 9-10 segmented. Uropod 1 slender, rami unequal, margins spinose. Uropod 2, rami marginally short-spinose; outer ramus <1/2 inner. Uropod 3 elongate, greatly exceeding telson; rami medium, unequal, marginally spinose. Telson subtriangular, length slightly less than twice width, apex narrowly rounded.

Brood plates medium broad, 5 narrow.

**Distributional Ecology:** *Apolochus barnardi* occurs in the *Phyllospadix* and *Egregia* sublittoral zone to depths of ~20 m, mainly on bottoms of coralline algae, stones, and sessile invertebrates, from Central to Southern California.

**Etymology:** The name is a tribute to the early recognition of this distinctive form by the late J. L. Barnard, and to his major contributions to knowledge of the North American Pacific amphipod fauna.

**Remarks:** *Apolochus barnardi* is distinct from *A. neopolitanus* DellaValle 1893, as figured by Krapp-Schickel (1982) in characters of the key (p. 13 ), It is also distinguished from *A. staudei* by characters of the key and as noted elsewhere (below).

### *Apolochus staudei* new species
(Fig. 7)

*Amphilochus neopolitanus* Della Valle, fide Staude, 1987: 379, fig. 18.40?;—Austin 1985: 593.
non: *Amphilochus neopolitanus* cf. Delle Valle fide Barnard 1962 (California).

**Material Examined**: 15 specimens at 7 stations:

**BRITISH COLUMBIA**
**North central coast, ELB Stns., 1964:**
H12, Stephens I., NW end (54°11'N, 130°48'W), *Phyllospadix*, kelp, LW, July 13. - 1 ♀; NMCC1992-0222. H20, McCauley I., NH end (53°43'N, 130°22'W), fine sand, LW, July 17 - 2 ♀♀, NMCC1992-0221. H21, N. end Banks I. (53°25'N, 130°10'W), 40-60 m. - 1 ♂ ; 2 ♀♀; NMCC1992-0223. H22, 1/2 mile off Larsen Hd., Banks I. (53°34'N, 130°34'W), kelp on sand and shell, 20 m dredge. July 17. -

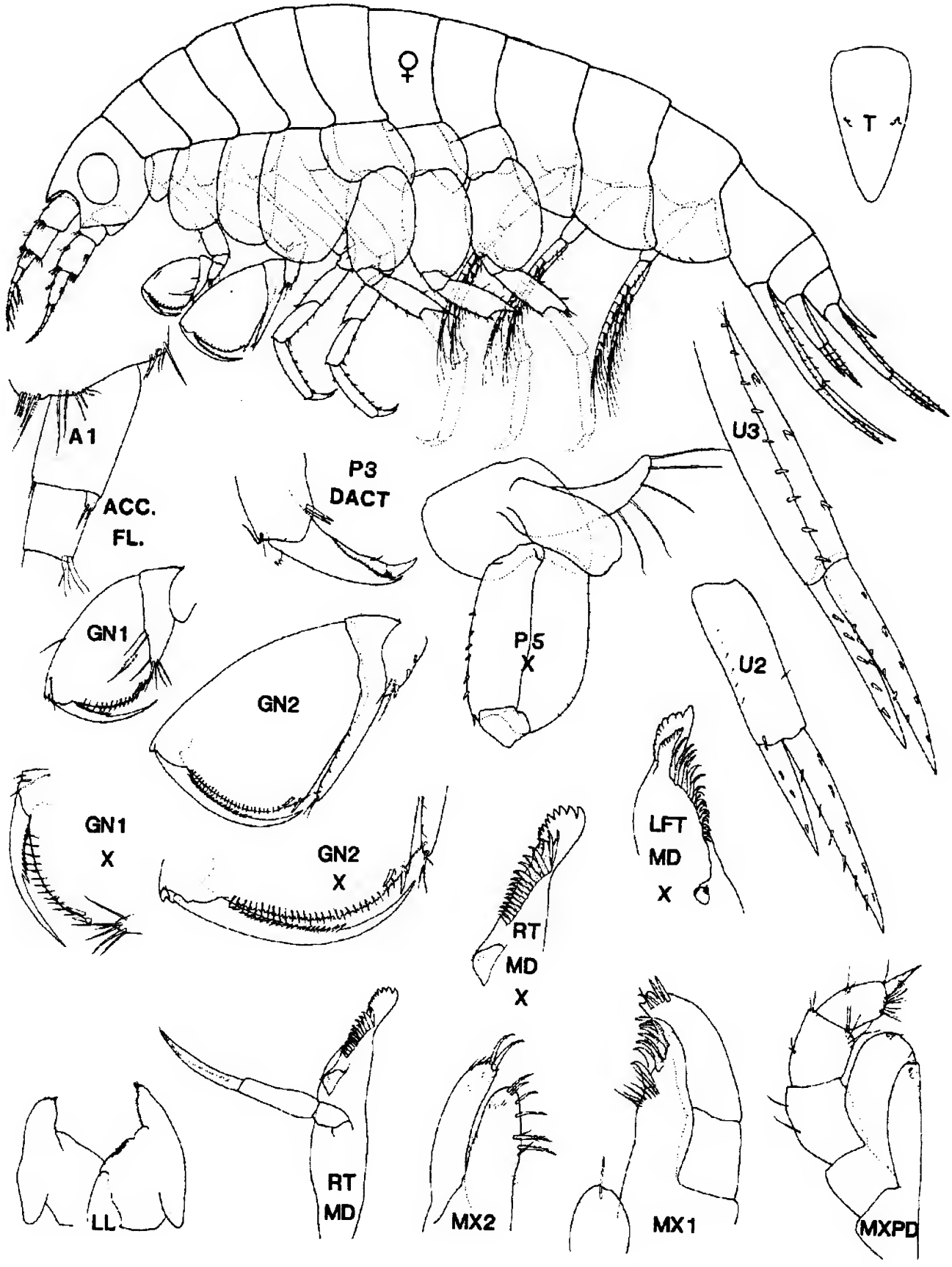



Fig. 7. **Apolochus staudei,** n. sp. Female ov. (2.4 mm) Holotype. N end of Rennison I., B. C.

1 ♀, 2 imm, NMCC-0224. H30, N. end of Rennison I. (52°51'N, 129°21'W), kelp and sand, 8-25 m dredge, July 20. - ♀ **Holotype** (slide mount); 34 ♀♀ **Paratypes,** 3 ♂♂ **Allotypes**, 9 im, **Paratypes**, NMCC1992-0226. H53,Townsend Pt., St. John Harbour (52°12'N, 128°28'W), *Phyllospadix*, kelp, *Corallina,* bedrock, LW, Aug. 7. - 1 ♀, NMCC1992-0230.

San Juan's Brown I., E. side, Queen Charlotte Str. ( 51°19'N, 127°46'W), 50-60 m dredge, FRB?, 1983. - 1 ♀, NMCC-1992-0253.

**Diagnosis:** Female ov. (2.4 mm) (holotype).

Rostrum medium. Eye large, subovate. Antennae short, subequal. Antenna 1, peduncular segment 1 & 2 short and deep, 3 small; flagellum 6-7 segmented; accessory flagellum minute. Antenna 2, flagellum 6-7 segmented.

Mandibular molar small, broadly triangular, with apical setules. Left mandible, lacinia 8-9 cuspate; spine row with 15-17 slender blades, distinctly largest distally; incisor multidentate; palp segment slightly longer than 2, inner margin finely pectinate, apex with single short seta. Maxilla 1, apical margin of inner plate nearly vertical, with 7 spine-teeth and 6-8 setae at inner angle; palp segments stout, segment 1 large. Maxilla 2, plates medium, inner plate with 6 marginal setae, proximally plumulose. Maxilliped, inner plate tall, narrow, apex subtruncate; outer plate medium broad, tall, inner margin smooth; palp segment 2 only slightly exceeding outer plate.

Coxa 1 short, little occluded by 2; coxae 2 -4 successively deepening, rounded below. Gnathopods 1 & 2 distinctly subchelate. Gnathopod 1, propod slightly expanding distally, palm convex, oblique; dactyl slender body denticulate behind, unguis elongate, slightly exceeding palmar angle; carpus narrow, lobe medium, extending about 1/2 posterior margin of propod. Gnathopod 2, propod large, broadening distally, palm convex, finely crenulate, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl slender, body finely pectinate behind, unguis elongate slightly exceeding palm; carpus short, posterior lobe elongate extending length of posterior margin of propod.

Peraeopods 3 & 4 medium, segment 6 with 4 posterior marginal spines; dactyls short, unguis short. Coxae 5-7 normally posterolobate, hind lobes acute below, margins unarmed. Peraeopods 5-7 regularly homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; dactyls short.

Pleon side plates 2 &3, gently convex below, hind corners not acuminate. Pleopod rami distinctly longer than peduncle, 9-10 segmented. Uropod 1 slender, rami slightly unequal, margins weakly spinose. Uropod 2, rami marginally short-spinose; outer ramus >1/2 inner. Uropod 3 elongate, greatly exceeding telson; rami medium, unequal, marginally spinose. Telson narrowly triangular, length about twice width, apex sharply rounded.

Brood plates medium broad; plate 5 narrow, with 5-6 longish distal marginal setae.

**Etymology:** The species name recognizes Dr. Craig P. Staude, Friday Harbor Laboratories, for his outstanding contribution to knowledge of the systematics and ecology of amphipods of the northeastern Pacific marine region.

**Distributional Ecology:** Known only from the Queen Charlotte Sound coast of north central British Columbia south to northern Queen Charlotte Strait, LW and shallow sublittoral to 60 m in depth.

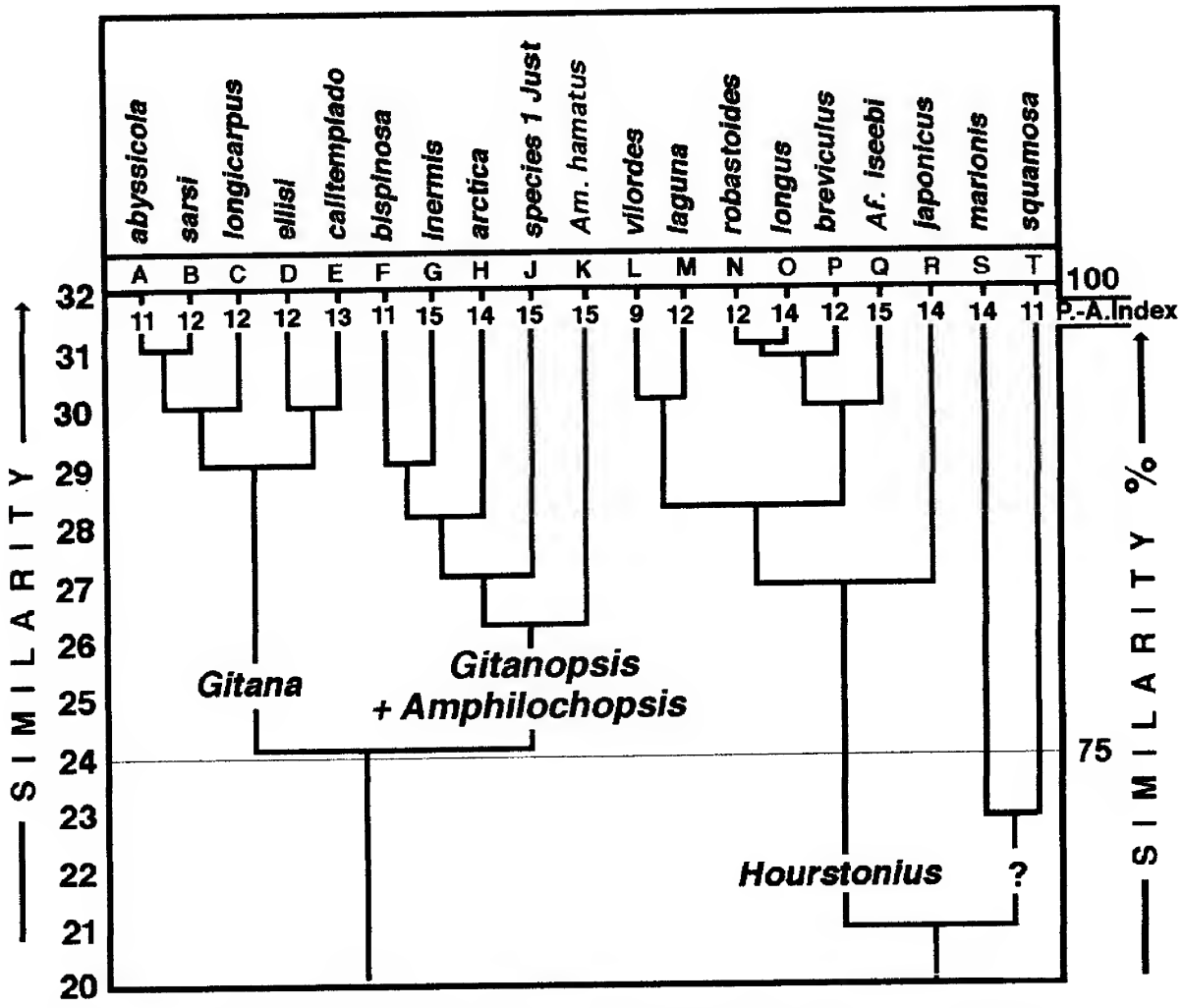
**Remarks:** Although most closely related to *A. barnardi, Amphilochus staudei* differs mainly in the form of the gnathopods, especially gnathopod 1, the distinctly posteriorly pectinate dactyls, the form of the maxilliped plates and palp, and the slightly longer and more acutely pointed telson.

## DISCUSSION

### Phyletic Reclassification

In phyletic revisions of the Gammaridea, family Amphilochidae has been placed within superfamily Leucothoidea (Bousfield 1979, 1982, 1983, 2000, 2001; Bousfield & Shih 1994). Lowry & Myers (2000) have recently proposed superfamily Iphimedioidea which combines former leucothoidean families Iphimedidae, Lafystiidae, and Laphystiopsidae with eusiroidean families Epimeridae and Amphithopsidae.

Remaining within Leucothoidea are families Leucothoidae, Anamixidae, Amphilochidae, Pleustidae, Stenothoidae, Thaumatelsonidae, and Cressidae. However, the Stenothoidae, Thaumatelsonidae, and Cressidae differ markedly in lacking a conspicuous rostrum, but exhibit sexually dimorphic gnathopods, strongly reduced maxilliped plates, frequent fusion of urosome segments and/or telson, and 2-segmented outer ramus of uropod 3. Furthermore, the gnathopods are frequently sexually dimorphic. Bousfield (2001b) formally utilizes the superfamily name Stenothoidea to encompass these three families. Based on the principal




Fig, 8. Phenogram of morphological similarities abnd possible phyletic relationships within *Gitana, Gitanopsis*, and *Hourstonius*.

character state differences noted above, and pending further detailed analysis, the superfamily name Stenothoidea is herewith formally recognized. Family Amphilochidae therefore remains within superfamily Leucothoidea.

**Reorganization of genera**

Taxonomic placement of species within northern hemispheric genera of amphilochid amphipods has long been unsatisfactory. Difficulties encountered, and partial generic revisions attempted by Lincoln (1979), Karaman (1980), and to some extent Krapp-Schickel (1982) and Hirayama (1983), are reflected in the number of character state "variables" specified by Barnard & Karaman (1991), especially within the genera *Gitana, Gitanopsis, Amphilochus*, and *Amphilochopsis*. Likewise, the present study encountered a persistence of unsatisfactory taxonomic categorizations within North Pacific species, and absence of previous numerical analysis. The authors have here attempted a realignment of species on more comprehensive and more natural generic conceptualizations.

The present treatment of species and genera utilizes a semi-phyletic modification of the UPGMA system of Sneath & Sokal (1973), as in previous analysis of other North Pacific amphipod groups (e.g., Jarrett & Bousfield 1994; Bousfield & Chevrier 1996). Character states are ordered plesio-apomorphically and relative phyletic placement of a taxon is represented by a numerical sum of plesiomorphic, intermediate, and apomorphic character states values (0, 1, and 2, resp.) in a Plesio-Apomorphic (P.-A.) Index. Tabular data on which the resulting phenograms are based are considered overly bulky and repetitive for publication here, but may be supplied on request.

Fig. 8 graphically portrays morphological similarities within species of *Gitana, Gitanopsis* sens. str. (effectively encompassing the arctic monotypic genus *Amphilochopsis*), and boreal-warm temperate, North Pacific and North Atlantic species of *Gitanopsis* (=

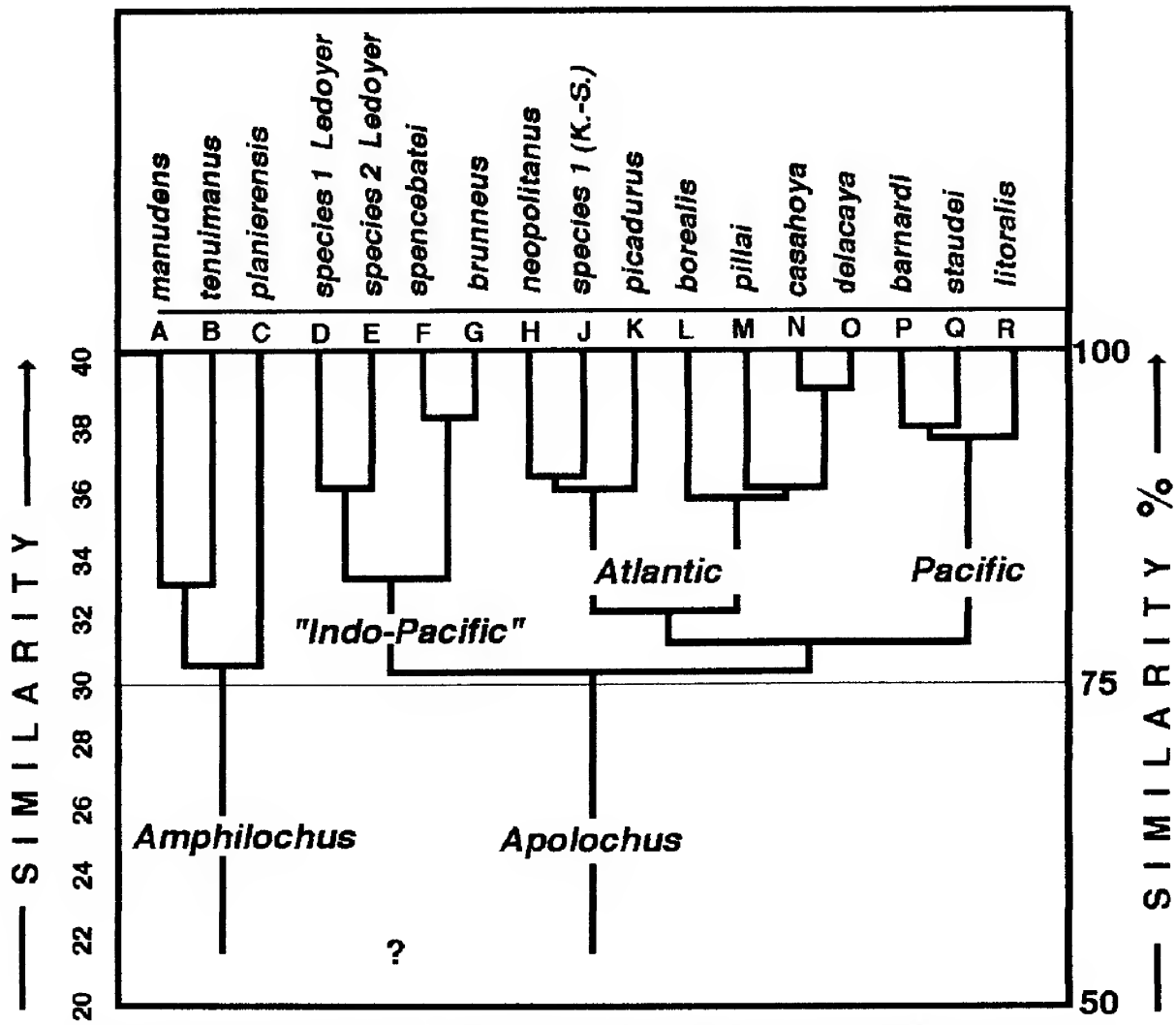



Fig. 9. Phenogram of morphological similarities and possible phyletic relationships within the genera *Amphilochus* and *Apolochus*.

*Hourstonius).* Species groupings are distinct above the 75% similarity level within *Gitana, Gitanopsis* sens. str., and *Hourstonius*. The former two genera cluster at about the 75% similarity level, with the genus *Amphilochopsis* somewhat intermediate between the two. However, the genus *Hourstonius* remains distinct below the 60% similarity level. The eastern Pacific species, *H. vilordes* (J.L. Barnard) is similar to species of both the western Pacific and Caribbean (Gulf of Mexico) regions, described mainly by Hirayama and McKinney, respectively. Not unexpectedly it is relatively remote from species of the South Atlantic (e.g., *H. magdai, H. squamosa)* described elsewhere.

This limited analysis tends to validate generic realignment of species within *Gitanopsis* Sars, 1895, and formal recognition of the generic concept *Hourstonius*. However, further study of relationships of species of the southern hemisphere, and of groups commensal with crustaceans, is clearly needed.

Fig. 9 portrays character state similarities within the North Atlantic genus *Amphilochus* Bate (sens. str.), based on the type species *A. manudens*, and species of the boreal-warm-temperate North Pacific, North Atlantic and Mediterranean-Indo-Pacific regions (= *Apolochus*, n. g.). Species groupings are distinct above the 75% similarity level within both groups, but the two genera remain distinct below the 50% similarity level. *Apolochus* here encompasses three subgroups: (1) an eastern Pacific complex of *A. litoralis* (Stout, 1912 ) and two closely similar species newly described herein; (2) a more speciose, essentially Atlantic (Caribbean-Mediterranean) subgroup encompassing A. *neopolitanus* Della Valle, *A. picadurus* (J. L. Barnard) and several superficially similar species [e.g., figured but unnamed by Lincoln (1979), Krapp-Schickel (1982)]; and (3) a Mediterranean Indo-Pacific subgroup encompassing *A. brunneus, A. spencebatei* and species attributed to "*A. neopolitanus*" by Ledoyer (1977).

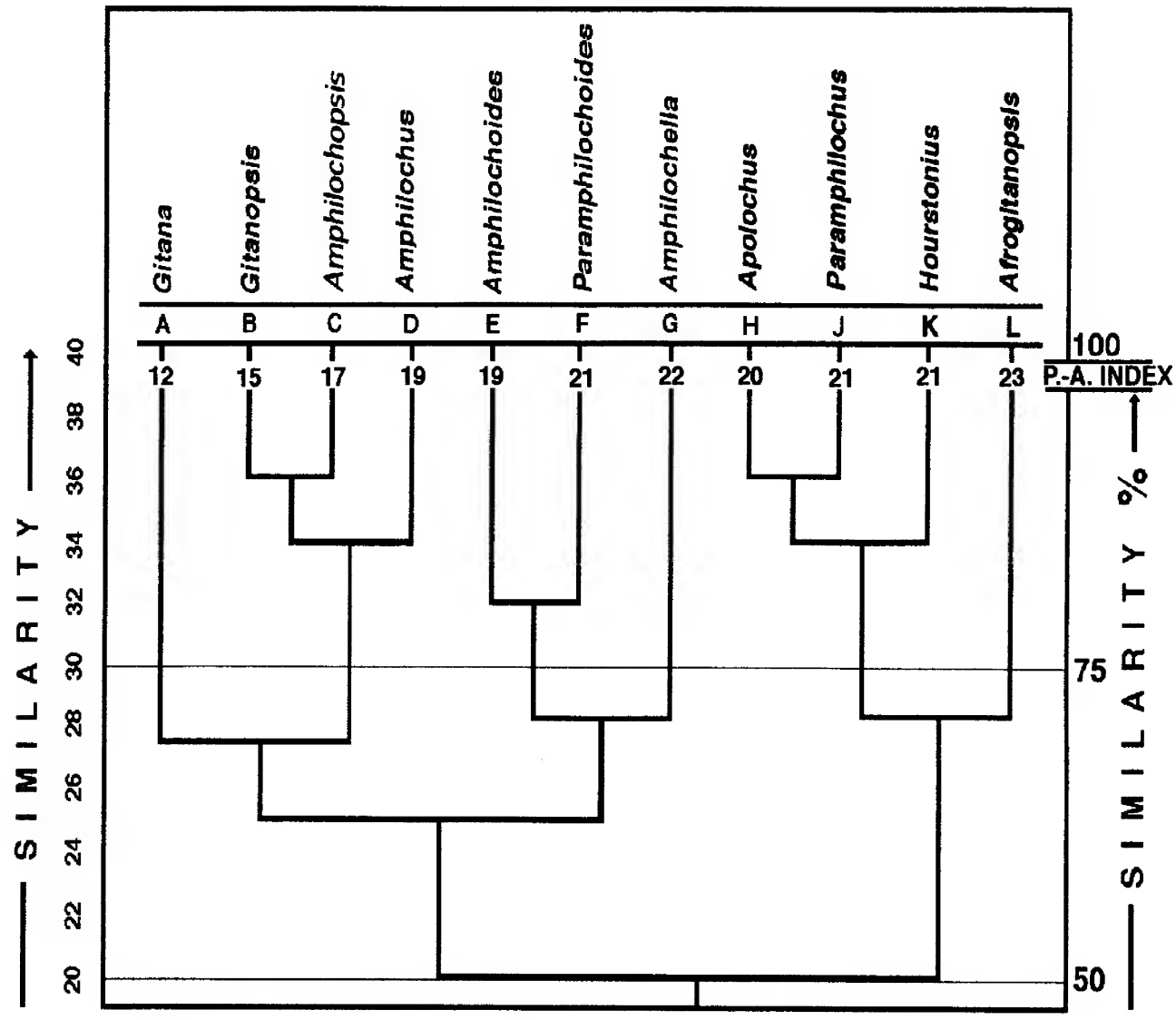



Fig. 10. Phenogram of morphological similarities and possible phyletic relationships within genera of Amphilochidae.

Species realignment within *Amphilochus* Sars, 1895, and formal recognition of the generic concept *Apolochus* seem clearly in order. Species attributable to genus *Apolochus* exhibit significantly higher A.-P. indices than the three more primitive species here attributed to *Amphilochus* Bate sens. str. However, further study, especially of Indo-Pacific regional taxa, is much needed.

Fig. 10 is a phenogram of morphological similarities within genera of family Amphilochidae, mainly of the northern hemisphere. The genera form three main subgroups at, or slightly below, the 75% similarity level: (1) an Arctic-North Atlantic complex of the primitive genus *Gitana* and the closely related *Gitanopsis, Amphilochopsis* and *Amphilochus,* having low P.-A. values ranging from 12 to 19; (2) a Mediterranean-Indian oceanic complex of advanced genera *Amphilochoides, Paramphilochoides* and *Amphillochella,* with intermediate P.-A. values of 19-21; and (3) a moderately advanced group of the closely related genera *Hourstonius* and *Apolochus* "satellite genera" *Paramphilochus* and *Afrogitanopsis* respectively, all with intermediate to high P.-A. values of 20-23. The two principal genera encompass about half the known species within the entire family.

The analysis further tends to confirm generic realignment of species within the new generic concepts of *Hourstonius* and *Apolochus.* The overall morphological closeness of these two genera underscores a need for use of multiple-character analysis, and avoidance of single- or few-character diagnoses, in defining taxonomic concepts at generic level and higher.

**Phyletic and Biogeographic Conclusions**

Members of family Amphilochidae are ectocommensals on gorgonians, hydroids and other sessile marine invertebrates. Their overall body and limb morphology is relatively primitive, in many ways similar to that of leucothoidean family Pleustidae. Such is expressed in the distinct rostrum, deep coxal plates, homopodous peraeopods, posterolobate coxae, and lanceolate uropod rami. However, morphological specializations including near-total loss of an accessory flagellum, modification of mouthparts for carnivory, and development of strongly subchelate gnathopods, are considered apomorphic.

Members of the primitive genus *Gitana* are mainly arctic-boreal and deep water, those of the more advanced genera *Gitanopsis* (sens. str.), *Amphilochopsis,* and *Amphilochus* (sens. str.) are actic-boreal and temperate, whereas those of the most advanced genera *Hourstonius*, *Apolochus* and *Paramphilochus* exhibit temperate, warm-temperate distributions in the northern hemisphere. These trends somewhat reflect the significance of higher phyletic classification in biogeographical relationships of North American marine amphipod taxa (Bousfield 2001). In this scenario, the most primitive higher taxa tend to occur mainly in Arctic waters, secondarily along the Pacific coast, and the most advanced taxa in the North Atlantic and Gulf regions. This phenomenon may reflect two major long-term evolutionary factors. Firstly, morphological evolution proceeds at a higher rate at higher ambient temperatures, and conversely at a lower rate at lower temperatures. Secondly, it may also reflect the long-term stability of a given marine region over geological time, wherein faunas of the ancient Pacific coast prove to be more primitive than those of the relatively recently developed North Atlantic Basin. As a corollary, the presence of ancient and relict coastal marine faunas within a higher taxon are more likely to be found in cold-temperate and Arctic regions, especially of long-term geological age. Conversely most highly advanced faunas are likely to be found in warm temperate and tropical regions, especially those of relatively recent geological origin.

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**Legend for Figures**

| | | | | | |
|---|---|---|---|---|---|
| A1 | - | antenna 1 | MD | - | mandible |
| A2 | - | antenna 2 | MX1 | - | maxilla 1 |
| ACC FL | - | accessory flagellum | MX2 | - | maxilla 2 |
| ABD | - | abdomen | MXPD | - | maxilliped |
| Br PL | - | brood lamella | P5-7 | - | peraeopods 5, 6, 7 |
| CX | - | coxal plate | PLP | - | pleopod |
| EP | - | abd. side plate | RT | - | right |
| GN1 | - | gnathopod 1 | SP | - | spine |
| GN2 | - | gnathopod 2 | T | - | telson |
| HD | - | head | U | - | uropod |
| LFT | - | left | ♂ | - | male |
| LL | - | lower lip (labium) | ♀ | - | female |